The watering of tall trees - Embolization and recovery

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Highlights

- Biologists are still debating tree recovery and the cohesion-tension theory.
- The concept of disjoining pressure is taken into account for high ascent of sap.
- Examples enable us to understand why the embolized vessels can be refilled.
- The stability domain of liquid thin-films limits the maximum height of trees.

Abstract: We can propound a thermo-mechanical understanding of the ascent of sap to the top of tall trees thanks to a comparison between experiments associated with the cohesion-tension theory and the disjoining pressure concept for liquid thin-films. When a segment of xylem is tight-filled with crude sap, the liquid pressure can be negative although the pressure in embolized vessels remains positive. Examples are given that illustrate how embolized vessels can be refilled and why the ascent of sap is possible even in the tallest trees avoiding the problem due to cavitation. However, the maximum height of trees is limited by the stability domain of liquid thin-films.

Keyword: tree recovery; sap ascent; disjoining pressure; cohesion-tension theory; high trees.
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Introduction

The crude sap ascends thanks to the negative pressure generated by the evaporation of water from the leaves. This classical explanation of the sap ascent phenomenon in tall trees is known as the cohesion-tension theory (Dixon and Joly (1894)) and is followed by a quantitative analysis of the sap motion proposed by van der Honert (1948). The main experimental check on the cohesion-tension theory comes from the Scholander pressure chamber (Scholander et al. (1955); Tyree et al. (2003)).
Trees pose multiple challenges for crude sap transfer:
Conditions in the sap do not approach the ultimate tensile strength of liquid water during transpiration (Herbert and Caupin (2005)). Nonetheless, the liquid water columns do break in tracheary elements. Cavitation events in the xylem seem to have been acoustically detected with ultrasonic transducers pressed against the external surface of the trees (Milburn and Johnson (1966),Tyree and Dixon (1983)). The porous vessel walls can prevent the gas bubbles from spreading and allow the flow to take alternate paths

around the emptied segments (Mercury and Shmulovich (2013)). The pores connecting adjacent segments in the xylem vessels pass through the vessel walls, and are bifurcated by bordered-pit membranes which are thin physical fluid-transmitters. Pit membranes in pores are of fundamental importance at nanometric scales; applying the Laplace formula, the pressure difference across them can easily be of the order of 1 - 10 MPa (Meyra et al. (1966); Jansen et al. (2009)). In the leaves and in the stems, the bordered-pit membranes serve as capillary seals that allow for a difference in pressure to exist between the liquid in the xylem and the gas phase outside (Tyree and Sperry (1989); Sperry (2013)). The pressure in water-containing neighbouring tracheids may still be negative; a considerable pressure drop therefore exists across the pit membranes (Choat et al. (2008)). No vessels are continuous from roots to stems, from stems to shoots, and from shoots to petioles, and the water does not leave a vessel in the axial direction but laterally along a long stretch (O'Brien and Carr (1970)).
Consequently, trees seem to live in unphysical conditions (Holbrook and Zwieniecki (1999, 2005)), and to be hydrated, they exploit liquid water in thermodynamically metastable states of negative pressure (Zwieniecki and Holbrook (2009)). At great elevation in trees, the value of the negative pressure increases the risk of cavitation and the formation of embolisms may cause a definitive break-down of the continuous column of sap, inducing leaf death. For a negative pressure $P_l = -0.6$ MPa in the sap, corresponding to an approximate minimal value of the hydrostatic pressure for embolism reversal in plants, we obtain a bubble radius $R \geq 0.24\,\mu\mathrm{m}$ (Nardini et al. (2011)); then, when all the vessels are tight-filled, nucleation sites naturally pre-existing in crude water may spontaneously embolize the tracheids (Pridgeon (1982)). Consequently, at high elevation, it does not seem possible to refill a tube full of vapour at a positive pressure when liquid-water must be at a negative pressure, but in the xylem, the liquid-water's metastability - due to negative pressures - may persist even in the absence of transpiration. Once embolized vessels have reached a nearly full state, is the refilling solution still at positive pressure, in mechanical equilibrium with some remaining air?

The most popular theory for the refilling process has been proposed by Holbrook and Zwieniecki in several papers: due to the fact that tracheary elements are generally in contact with numerous living cells (Zimmermann (1983)), they hypothesized that crude sap is released into the vessel lumen from the adjacent living cells in a manner similar to root exudation (Kramer and Boyer (1995)) and they assumed that the mechanism for water movement into embolized conduits involves the active secretion of solutes by the living cells. However, a survey across species indicated the root pressure could reach 0.1-0.2 MPa above atmospheric pressure (Fisher et al (1997)) and was the only logical source of embolized vessels' repairing at night in smaller species with well-hydrated soil. The Münch pumping mechanism (Münch (1930)) was invoked, but basic challenges for this mechanism still persisted: osmotic pressures measured in sieve tubes do not scale with the height of a plant as one would expect (Turgeon (2010); Johnson and Canny (2013)) and such scenarios have not yet been empirically verified. Hydraulic isolation was also required to permit the local creation of the positive pressures necessary to force the gas into solution yet the embolism removal might be concurrent with tree transpiration (Zwieniecki and Holbrook (1998)). Additionally, refilling in the presence of tension in adjacent vessels required the induction of an energy-dissipating process that would locally pump liquid into the emptied vessels (Canny (1997)) or lower the water potential in the vessel with the secretion of solutes (Zwieniecki and Holbrook (2009)). As a consequence, Canny (2001); Canny et al. (2007); Johnson and Canny (2013) and other authors (McCully et al. (1998)) suggested that alternative mechanisms might be required.

Alternatively, for slightly compressible liquids, the molecular theory of capillarity, applied to liquid thin-films wetting solid substrates, demonstrates an unexpected behaviour in which liquids do not transmit the pressure to all their connected parts, as it is for liquid-bulk parts (Dzyaloshinsky et al. (1961)). Consequently, it is possible to obtain an equilibrium between connected liquid parts where one is at a positive pressure - the pressure in a liquid thin-film - and the other one is at a negative pressure - the pressure in the liquid bulk. The vapour-gas phase in contact with the liquid thin-film is at the same positive pressure as the liquid thin-film. The refilling of xylem is not in contradiction with possible phase equilibria at different pressures in the stems. The model associated with this behaviour corresponds to the so-called *disjoining pressure theory*.

The paper analyses the results obtained in the physical chemistry literature that are useful to explain the refilling of tracheary elements and the watering of tall trees. The apparent incompatibility between the model in Gouin (2008) and the cohesion-tension theory is now solved. The model allows to explain aspects of sap movement which the classical cohesion-tension theory was hitherto unable to satisfactorily account for, e.g. the refilling of the vessels in spring, in the morning or after embolism events, as well as the compatibility with thermodynamics' principles.
The paper is organized as follows: Section 1 is required by the fact that nanofluidic and liquid thin-films concepts are fundamental physical tools for the rest of the paper. Following Derjaguin's Russian school of physical chemistry, we propose an experimental overview of the disjoining pressure concept for liquid thin-films at equilibrium. Thermodynamical potentials are also recalled for liquid thin-films. We end the section by a study of vertical motions along liquid thin-films: a comparison between liquid-motions' behaviours both in tight-filled microtubes and in liquid thin-films is proposed. It appears that slippage conditions on walls multiply the flow rate along liquid thin-films by an order ranging from 10^2 to 10^4 and consequently, liquid thin-films flow-rate is not similar to Poiseuille's liquid-flow-rate.
Section 2 is the most important - and completely new - part of this research. The section focuses on trees containing vessels considered as machines. From experiments presented in the previous section, a model of xylem using liquid thin-films is proposed. Such a model of xylem allows to explain both the thermodynamical consistence of the cohesion-tension theory and the conditions of the crude-sap refilling at high elevation. This previous *thought experiment* is modified to take account of air-vapour pockets: when the air-vapour pocket pressure is greater than the air-vapour bulk pressure, a huge flow occurs between the two parts filled by air-vapour gas to empty the air-vapour pockets although the liquid-bulk pressure is negative.
Section 3 is a byproduct of section 1. The section shortly reproduces results we previously published in the literature and it is an important complement to Section 2. The *pancake-layer concept*, associated with the breaking down of vertical liquid thin-films, allows to forecast the limit of validity of the model and yields a maximum height for the tallest trees.
A conclusion ends the article; this section suggests experiments to verify the accuracy of sap ascent for tall trees and the accuracy of crude-sap's refilling.

1. The disjoining pressure for liquid thin-films

The disjoining pressure is a physical concept specific to liquid thin-films wetting a flat solid surface and bordered by a vapour bulk. A complete description is proposed by Derjaguin et al. (1987). Liquids in contact with solids are submitted to intermolecular

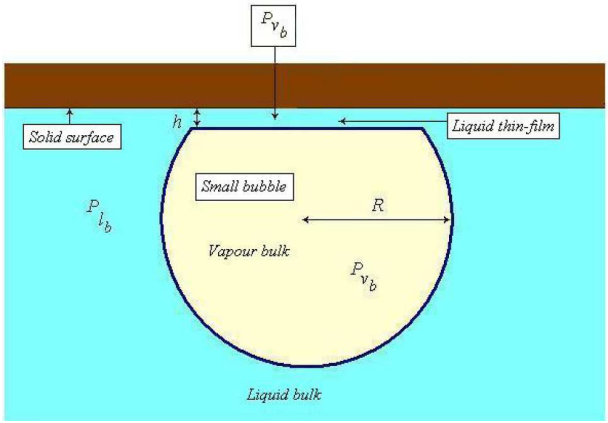

FIGURE 1. *The bubble method of determining the disjoining pressure isotherms of wetting films.* The hydrostatic pressure in the liquid thin-film is the same as in the microscopic bubble and is different from the liquid-bulk pressure (from Derjaguin et al. (1987), page 330).

forces making liquids a little compressible and consequently heterogeneous; the stress tensor is non-spherical contrary to what it is in homogeneous bulks (Gouin (1998)).

1.1. *Horizontal liquid thin-films*

At a *given temperature* T_0, two experiments allow to understand the physical meaning of horizontal liquid thin-films *at equilibrium*:

• The first experiment explaining the concept was carefully described in Derjaguin et al. (1987): a liquid bulk submitted to pressure p_{l_b} contains a microscopic bubble of radius R contiguous to a solid (Fig. 1). The bubble floats upward and approaches a horizontal smooth plate, and a planar liquid thin-film is formed after some time. The liquid thin-film separates the flat part of the bubble, which is squeezed onto the solid surface, from inside. Inside the bubble, the pressure of the vapour bulk is p_{v_b}. The film is thin enough for gravity to be neglected thickness-wise and the hydrostatic pressure of the liquid thin-film is identical to the vapour-bulk pressure inside the bubble. Pressure p_{v_b} differs from pressure p_{l_b} of the contiguous liquid bulk. The previous analysis can apply to the bulk pressure p_{l_b} in the liquid a short distance away from the surface; the bulk pressure p_{l_b} is not really affected by the gravity gradient because of the microscopic size of the bubble which remains spherical outside the liquid thin-film. By using the Laplace formula, the difference between the two bulk pressures is

$$p_{v_b} - p_{l_b} = \frac{2\gamma}{R}, \tag{1.1}$$

where γ is the surface tension of the bubble liquid-vapour interface. Pressure p_{v_b} in vapour bulk (v_b) of density ρ_{v_b} (*mother vapour-bulk*), and pressure p_{l_b} in liquid bulk (l_b) of density ρ_{l_b} (*mother liquid-bulk*), from which the liquid thin-film extends, create the pressure difference already estimated in (1.1) and named $\Pi(h)$:

$$\Pi(h) = p_{v_b} - p_{l_b}\,. \tag{1.2}$$

This interlayer pressure $\Pi(h)$ additional to the mother liquid-bulk pressure is called the *disjoining pressure* of the thin film of thickness h, and curve $h \longrightarrow \Pi(h)$ - obtained by changing the bubble's radius and thereby film thickness h - is the *disjoining pressure isotherm.*

Derjaguin's clever idea was to create an analogy between liquid thin-films and liquid-

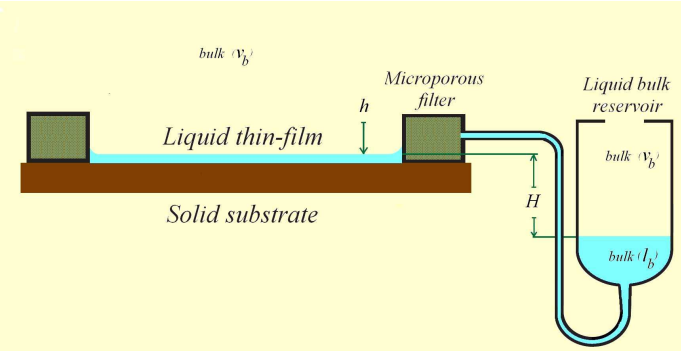

FIGURE 2. *Diagram of the technique for determining the disjoining pressure isotherms of wetting thin-films on a solid substrate.* A circular wetting thin-film is formed on a flat substrate to which a microporous filter with a cylindrical hole is clamped. A pipe connects the filter filled with the liquid to a reservoir containing the mother liquid-bulk that can be moved by a micrometric device. The disjoining pressure is equal to $\Pi = (\rho_{l_b} - \rho_{v_b})\, gH$, where g is the gravity acceleration (from Derjaguin et al. (1987), page 332).

vapour interfaces of bubbles. Liquid thin-films - allowing to obtain an equilibrium between fluid phases at different pressures - are physically similar to "bubbles' flat interfaces". The pressure in the liquid phase is different from the liquid pressure in the liquid thin-film, which is the same as the pressure in the vapour phase; thereby, the liquid - with a very small compressibility - does not completely transmit the pressure in all places where it lays.

• The second experiment illustrating the disjoining pressure concept is associated with the classical apparatus due to Sheludko (1967) and is described in Fig. 2. The hydrostatic pressure in the liquid thin-film located between a solid wall and a vapour bulk (v_b) differs from the pressure in contiguous liquid bulk (l_b).

As done in the first experiment, the disjoining pressure is equal to the difference between thin-film's interfacial surface pressure p_{v_b} - which is the pressure of the mother vapour-bulk - and mother liquid-bulk's pressure p_{l_b}. As explained below in Subsection 1.2, the forces arising during the thinning of a film of uniform thickness h produce disjoining pressure $\Pi(h)$ in the thin film according to the surrounding bulks.

1.2. *Chemical potential, Helmoltz's free energy and their consequences*

The chemical potential of a fluid is a versatile thermodynamical potential allowing to study the equilibrium between vapour and liquid bulks. At a given temperature T_0 - due to the pressure state-equation - the chemical potential of the fluid can be considered as a function of fluid density ρ (Rowlinson and Widom (1984)). We choose - as reference chemical potential - μ_0 which is null in the bulks of the phase equilibrium associated with the planar vapour-liquid interface:

$$\mu_0(\rho_v) = \mu_0(\rho_l) = 0,$$

where ρ_v and ρ_l are the vapour and the liquid bulk-densities, respectively. The densities in the mother bulks are connected by the relation

$$\mu_0(\rho_{v_b}) = \mu_0(\rho_{l_b})$$

and the pressure is

$$p(\rho) = \rho\, \mu_0(\rho) - \Psi_0(\rho) + p_0,$$

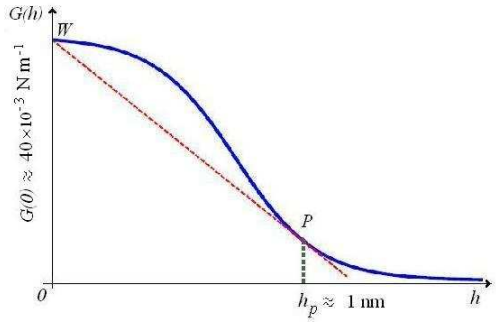

FIGURE 3. *Sketch of the pancake layer thickness for water.* The construction of the tangent to curve $G(h)$ issued from point W of coordinates $(0, G(0))$ yields point P; point W is associated with a high-energy surface of the dry wall and point P is associated with pancake-thickness h_p (de Gennes et al. (2004)). The values indicated for h_p and $G(0)$ are approximatively those of water at 20°Celsius: the wetting film damping a solid wall is stable down to $h_p \approx 1$ nm.

where p_0 is the pressure of planar liquid-vapour equilibrium, and due to thermodynamical relations (Callen (1985)),

$$\Psi_0(\rho) = \int_{\rho_v}^{\rho} \mu_0(\tau)\, d\tau$$

is the Helmoltz free energy per unit volume, where in the integral, variable τ is the variable of integration. When the fluid is water, the Helmoltz free energy per unit volume is classically called the water potential.

As described in Derjaguin et al. (1987), Chapter 2 and de Gennes et al. (2004), Chapter 4, the thermodynamic potential or Gibbs free-energy (per unit area) of the liquid thin-film is noted G and can be expressed as a function of h. In a reversible equilibrium change at constant temperature and constant pressures, accompanied by a change dh in the interlayer thickness, the external forces do work like $-\Pi(h)\, dh$ and this work must be equal to the increment dG of the thermodynamical potential. Hence, thanks to the relation

$$\Pi(h) = -\left(\frac{\partial G}{\partial h}\right),$$

the partial derivative being taken at constant temperature and pressures, we can write G in the form

$$G(h) = \int_{h}^{+\infty} \Pi(\tau)\, d\tau,$$

where $h = 0$ is associated with a dry wall in contact with the mother vapour-bulk, $h = +\infty$ is associated with a wall in contact with the mother liquid-bulk when the value of G is equal to 0; variable τ is the variable of integration.

For liquid water wetting the solid wall constituted with different substrates, experiments and calculations are proposed in Sheludko (1967). The liquid thin-film thickness depends on the disjoining pressure value: for water at 20°Celsius and a disjoining pressure value of an order of several atmospheres, the order of thickness is of some nanometres and the liquid thin-film is a nanolayer. In the liquid thin-film, the liquid is inhomogeneous: the variation of the liquid density is of the order of 4/100 over a distance of some nanometres, but the density gradient is important (its order is about 10^{12} $\mathtt{kg.m}^{-4}$).

The coexistence of two adjacent liquid film-segments with different thicknesses is a phenomenon which can be represented by the equalities of chemical potentials and superficial tensions of the two films. A spectacular case corresponds to the coexistence of a liquid

thin-film of thickness h_p and the dry solid wall. The liquid thin-film is the so-called pancake layer and corresponds to the minimal thickness for which a stable wetting film damps a solid wall. The minimal thickness h_p satisfies the relation

$$G(0) = G(h_p) + h_p\,\Pi(h_p). \tag{1.3}$$

The geometrical interpretation of Eq. (1.3) is proposed on Fig. 3.

1.3. *Vertical liquid thin-films*

The experiments in Subsection 1.1 and definitions in Subsection 1.2 can be extended to vertical liquid thin-films wetting a vertical solid surface (we propose a complete study in Gouin (2009)). We denote x the coordinate along the upward-vertical direction and g the gravity acceleration. When altitude differences are of one hundred meter order, the fluid densities in mother bulks at level x, (l_{b_x}) and (v_{b_x}) are not perceptibly modified and they are always denoted ρ_{l_b} and ρ_{v_b}. The vapour pressure is not perceptibly changed; the mother bulk (v_{b_x}) is the same as (v_{b_0}) and will be always denoted (v_b). The modifications are associated with a new chemical potential denoted μ_x at level x and the liquid pressure,

$$\mu_x = \mu_0 + g\,x, \qquad p_{l_{b_x}} \simeq p_{l_{b_0}} - \rho_{l_b} g\,x\,.$$

Consequently, the disjoining pressure strongly depends on the liquid thin-film altitude. The disjoining pressure can be considered as a function of x and if the disjoining pressure is zero at reference level, we obtain (Gouin (2009)),

$$\Pi(h_x) \simeq \rho_{l_b} g\,x\,. \tag{1.4}$$

To make it clear, we draw a diagram on Fig. 4. A reservoir along the solid wall is connected with the liquid thin-film at different levels. The liquid thin-film has a thickness h_x depending on the altitude. At equilibrium the disjoining pressure can interchangeably be written

$$\Pi(h_x) = \Pi[x] \tag{1.5}$$

where - for the sake of simplicity - Π is a function of x as indicated in (1.4) as well as another function of h_x as proposed in (1.2). Relation (1.5) defines the connection between x-level and h_x-thickness.

1.4. *Motions in the liquid thin-films*

The results arising from molecular physics allow to study the motions of liquid thin-films of a thickness of some nanometers (Oron et al. (1997); Gouin and Gavrilyuk (2008)). There are qualitative experiments for slippage on solid wall when the film thickness is of the mean free path order (Churaev (1996)). The boundary condition on the wall writes

$$\boldsymbol{u} = L_s\, d\boldsymbol{u}/dn,$$

where $\boldsymbol{u}$ is the liquid velocity, $d\boldsymbol{u}/dn$ is the normal derivative at the wall and L_s is the so-called *Navier length* (de Gennes (2002)). The Navier length may be as large as a few microns (Tabeling, ed. (2004)), and we obtained the mean liquid velocity $\overline{\mathbf{u}}$ along a vertical liquid thin-film in Gouin (2011) :

$$\nu\,\overline{\mathbf{u}} = h_x \left(\frac{h_x}{3} + L_s\right) [\,\mathbf{grad}\ \Pi(h_x) - g\,\boldsymbol{i}\,], \tag{1.6}$$

where ν denotes the kinematic viscosity and $\boldsymbol{i}$ the vertical unit vector (we simply note that for horizontal liquid thin-films, $g = 0$). The increase in disjoining pressure comes from the decreasing thickness of the liquid thin-film creating the upward liquid motion.

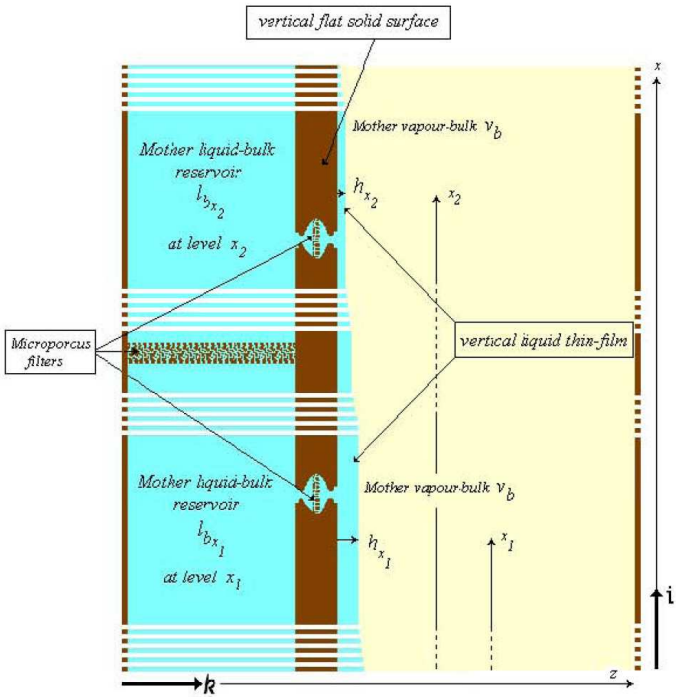

FIGURE 4. *Diagram of a vertical liquid thin-film.* A liquid thin-film bordered by a mother vapour-bulk (v_b) wets a vertical flat solid surface. Mother liquid-bulk (l_{b_x}), but not (v_b), depends on the x-level. Like on Sheludko's apparatus, microporous filters connect the mother-bulk reservoir at different altitudes with the liquid thin-film. The different parts of the mother-bulk reservoir can also be connected by microporous filters.

The slippage condition multiplies the flow rate along liquid thin-films by a factor of $(1+3L_s/h_x)$. For example, if $h_x = 3\,\mathtt{nm}$ and $L_s = 100\,\mathtt{nm}$, which is a Navier length of small magnitude with respect to experiments, the multiplicative factor is 10^2; if $L_s = 7\,\mu\mathtt{m}$, as considered in Tabeling, ed. (2004), the multiplicative factor is 10^4 which is of the same order as in nanotube calculations (Gouin (2012); Garajeu et al. (2013)), and observations (Mattia and Gogotsi (2008)).

2. Embolization and recovery

Since the beginning of the cohesion-tension theory, many efforts have been done to understand sap motions in the vascular network and to replicate tree functions when vessels are under tension. Synthetic systems simulating the transport processes have played an important role in model testing, and methods creating microfluidic structures to mimic tree vasculature have been developed (Stone et al. (2004)); by using synthetic hydrogel, which plays the role of the pit membrane, Wheeler and Stroock (2008) captured some fundamental aspect of the xylem tension and flow.

Liquid thin-films of some nanometre thickness can be considered as plane interlayers with respect to the diameters of capillary vessels, which range from 10 to 500 μm. Adjacent xylem walls are connected by active bordered-pit membranes with micropores (Meyra et al. (1966)). The membranes separate two volumes of fluid, and generally refer to lipid bilayers that surround living cells or intracellular compartments (Stroock et al. (2014)). The micropores are a few tens of microns wide. Due to the meniscus curvatures at microp-

ore apertures, marking off liquid-water bulk from air-vapour atmosphere, the water-bulk pressure is negative inside micropore reservoirs, but, surprisingly, semi-permeable micropores allow flows of liquid-water at negative pressure to be pushed toward air-vapour domains at positive pressure (Tyree and Zimmermann (2002)).
Water exits the leaves by evaporation through stomata into subsaturated air. Resistance of the stomata sits in the path of vapour diffusion between the interior surfaces of leaves and the atmosphere but many of the tallest trees appear to lack active loading mechanisms (Fu et al. (2011)). When active transpiration occurs, stomata are open and these pumps run. The growth and degrowth of bubbles is rapid within xylem segments, but at night, although the stomata are closed, xylem vessels developing embolies during the day can be refilled with liquid-water and the metastability of the liquid-water may persist even in the absence of transpiration (Zwieniecki and Holbrook (1998); Zufferey et al. (2011)). It is interesting to note that optical measurements indicate capillary Young's contact-angles of about 50° for water on the xylem at 20°Celsius †, suggesting that the xylem walls are not fully wetting and the capillary spreading cannot really aid the liquid-water refilling but may explain the apparent segregation of liquid-water into droplets (Zwieniecki and Holbrook (2000)).

2.1. *A diagram of vessel elements for tall trees*

At usual temperature (for example 20°Celsius), we consider two vertical adjacent vessels linked by micropore reservoirs at convenient negative pressures - in the same physical conditions of Subsection 1.3 - and with pit membranes dotting their walls (the bordered-pit membranes of the order of several tens of nanometres correspond to the microporous filters in Fig. 4). The mother liquid-water bulk also contains dissolved air and the mother vapor-bulk contains air ‡.
One vessel - corresponding to subsaturated mother air-vapour bulk - is embolized with a positive pressure; it generates a liquid thin-film which wets the xylem wall (see the upper part of Fig. 5). The other vessel is filled with the mother liquid-water bulk at a negative pressure linked to the liquid thin-film thanks to a micropore reservoir with a bordered-pit membrane (see the lower part of Fig. 5). Such a system can be in equilibrium, although the pressure is not the same in the two adjacent vessels.
In the same configuration, the vessel elements are now assumed to be weakly out-of-equilibrium. As explained in Subsection 1.4, the driving force of the sap ascent comes from the decreasing thickness of the liquid thin-film wetting the walls in the embolized vessels; consequently the negative pressure value of the mother liquid-water bulk in micropore reservoirs decreases (its absolute value increases). Additionally, air-vapour pockets can coexist with the mother liquid-water bulk of one of the two vessels. The air-vapour pockets also generate liquid thin-films bordering xylem walls (see Fig. 5).
Due to their curvature, the pressures of air-vapour pockets are generally higher than the mother vapor-bulk pressure in the other vessel. As proposed in the caption of Fig. 5, the vapour pockets and their liquid thin-films empty into the vessel with the lower air-vapour bulk pressure. The analogy proposed in Subsection 1.1 between liquid thin-

† This value is also an arithmetic average of different Young angles proposed in the literature (Mattia and Gogotsi (2008)).

‡ An important property of any fluid mixture consisting of liquid water, its vapour and air allows to directly take the results of Section 1 into account (Gouin (1990)). The mixture's total pressure is the sum of the partial pressures of the components, and at equilibrium the partial pressure of air is constant through liquid-air and vapour-air domains. Consequently, results from Section 1 are unchanged: the disjoining pressure of the mixture is the same as for fluid without air when a liquid thin-film only separates liquid and vapour bulks (Gouin (2009)).

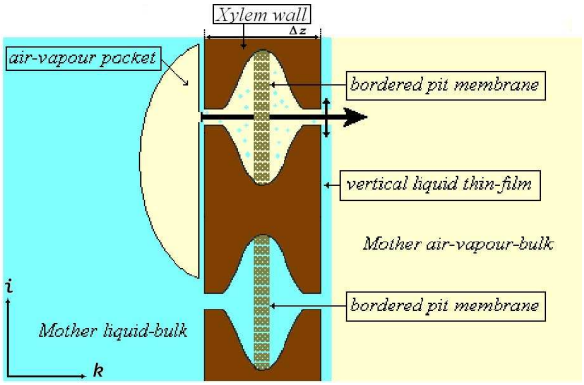

FIGURE 5. At equilibrium between bulks at altitude x, mother liquid-bulk (l_{b_x}) balances the liquid thin-film and mother air-vapour-bulk (v_b). It is not true for the vapour pocket and the mother air-vapour-bulk: when the pressure in the air-vapour pocket is greater than the pressure in mother air-vapour-bulk, the air-vapour pocket empties into the mother air-vapour-bulk.

films and liquid-vapour interfaces of bubbles allows to simply understand the motion directions between air-vapour pockets and the mother air-vapour bulk: for example, when two bubbles are included in a liquid bulk (corresponding to the mother liquid-water bulk at negative pressure), the smallest bubble with the greatest pressure (i.e. the air-vapour pocket) empties into the largest bubble with the lowest pressure (i.e. the air-vapour bulk of the embolized vessel) (McCarthy (1988)).
Such events happen in particular at night, when - due to the absence of evaporation - the vapor is subsaturated in embolized vessels; the curvature of the air-vapor pockets generates a pressure greater than the pressure in the embolized vessels. Conversely, during the day and strong sunlight, the vapour in vessels is saturated by evaporation; the air-vapour pressure increases in the embolized vessels and the air-vapor gas must flow back into the vessels with air-vapour pockets of subsaturated vapour included in the mother liquid-water bulk at negative pressure.

2.2. *Estimation of the transfer of masses between air-vapour pockets and air-vapour bulk*

It is interesting to estimate the magnitude of the air-vapour flow between air-vapour pockets and the mother air-vapour bulk. At altitude x, the mother bulks are still named (l_{b_x}) and (v_b), respectively and as indicated in footnote, the disjoining pressure value has the same value as in Section 1.
At equilibrium between the two mother bulks, the vertical liquid thin-film - the liquid thin-film between the mother air-vapour bulk and the xylem wall - is also in equilibrium and at the same pressure as the mother air-vapour bulk. Depending on reservoir altitude x, the mother liquid-bulk can be at negative pressure. In that case, the pressure in the air-vapour pocket is *assumed to be greater* than the pressure in the mother air-vapour bulk. Consequently, the air-vapour pocket and the mother air-vapour bulk are not in equilibrium. Nonetheless, the air-vapour pocket and the mother liquid-bulk may be at equilibrium, with a liquid thin-film separating the air-vapour pocket and the xylem wall; the liquid thin-film between the air-vapour pocket and the xylem wall is thinner than the liquid thin-film between the mother air-vapour bulk and the xylem wall.
In the case of perfect fluids, the equation of motion is deduced from Serrin (1959) and Gouin (1987). Due to the fact that the chemical potential of the air-component is constant, we get:

$$\boldsymbol{a} + \mathrm{grad}(\mu_{_0} + g\,x) = 0, \tag{2.1}$$

where μ_0 is the chemical potential of the water-component, not constant but depending on the density value and $\boldsymbol{a}$ is the acceleration. As presented on Fig. 4, distance x corresponds to the ascending vertical height. Let us note that in the equilibrium case, Eq. (2.1) writes

$$\mu_0 + g\,x = c_0,$$

classically corresponding to a connection between altitude x and chemical potential μ_0 (c_0 is constant); in perfect motion, only acceleration term $\boldsymbol{a}$ must be added to $\mathrm{grad}(\mu_0 + g\,x)$. Expansions of μ_0 at the first order in the mother bulks write (Gouin (2009)),

$$\mu_0(\rho) \approx \frac{c_v^2}{\rho_v}(\rho - \rho_{v_b}), \qquad \text{in the air-vapour phase,} \tag{2.2}$$

$$\mu_0(\rho) \approx \frac{c_l^2}{\rho_l}(\rho - \rho_{l_b}), \qquad \text{in the liquid phase,} \tag{2.3}$$

where c_v and c_l are the isothermal sound velocity of the air-vapour mixture and the liquid-water, respectively. The proofs of (2.2) and (2.3) are deduced from $\partial\mu_0/\partial\rho \equiv (1/\rho)\,(\partial p/\partial\rho)$, where $\partial p/\partial\rho$ are the values of the square of the isothermal sound velocity of the fluid at density ρ, taken in the vicinity of $\rho_{v_b} \approx \rho_v$ and $\rho_{l_b} \approx \rho_l$, respectively. Consequently, the motion equations in the air-vapour mixture and in the liquid are:

$$\boldsymbol{a} = -\frac{c_v^2}{\rho_v}\,\mathrm{grad}\,\rho - g\,\boldsymbol{i}, \qquad \text{in the air-vapour phase,}$$

$$\boldsymbol{a} = -\frac{c_l^2}{\rho_l}\,\mathrm{grad}\,\rho - g\,\boldsymbol{i}, \qquad \text{in the liquid phase,}$$

Components $\boldsymbol{a}.\boldsymbol{i}$ are equal in the two phases: $\boldsymbol{a}.\boldsymbol{i} = -g \approx -10\ \mathtt{m}\,.\,\mathtt{s}^{-2}$. Components $\boldsymbol{a}.\boldsymbol{k}$ are different:

$$\boldsymbol{a}.\boldsymbol{k} = -\frac{c_v^2}{\rho_v}\,\frac{\partial\rho}{\partial z} \approx -\frac{c_v^2}{\rho_v}\,\frac{\Delta\rho}{\Delta z}, \qquad \text{in the air-vapour phase,} \tag{2.4}$$

$$\boldsymbol{a}.\boldsymbol{k} = -\frac{c_l^2}{\rho_l}\,\frac{\partial\rho}{\partial z} \approx -\frac{c_l^2}{\rho_l}\,\frac{\Delta\rho}{\Delta z}, \qquad \text{in the liquid phase,} \tag{2.5}$$

where $\boldsymbol{k}$ is the normal-outward unit vector to the vertical wall and z is the associated coordinate. In (2.4), $\Delta\rho$ represents the difference of densities between the air-vapour pocket and the mother air-vapour bulk and in (2.5), $\Delta\rho$ represents the difference of densities between the liquid thin-film squeezed between the air-vapour pocket and the vertical liquid thin-film; Δz is an estimation of the distance between the air-vapour pocket and the air-vapour bulk.
The physical values of the isothermal sound velocity, $c_v \approx 3 \times 10^2\ \mathtt{m\ s}^{-1}$ and $c_l \approx 1.5 \times 10^3\ \mathtt{m\ s}^{-1}$, are given in the Handbook of Chemistry and Physics (1984). We assume the following conditions to be corresponding to a pressure in the air-vapour pocket slightly greater than the mother air-vapour pressure:

$$\Delta z \approx 10^{-3}\ \mathtt{m}, \quad \Delta\rho/\rho_v \approx 10^{-2}, \quad \Delta\rho/\rho_l \approx 10^{-3}.$$

We get:

$$\boldsymbol{a}.\boldsymbol{k} \approx 10^6\ \mathtt{m\ s}^{-2}, \qquad \text{in the air-vapour phase,}$$

$$\boldsymbol{a}.\boldsymbol{k} \approx 2 \times 10^7\ \mathtt{m\ s}^{-2}, \qquad \text{in the liquid phase.}$$

We obtain an outsized acceleration for air-vapour gas - between the air-vapour pocket and its associated liquid thin-film - directed towards the mother air-vapour bulk. The air-vapour pocket empties into the mother air-vapour bulk. One notes that the acceleration

in the liquid thin-film is an order higher than the acceleration in air-vapour gas. The liquid thin-film associated with the air-vapour pocket empties faster than the air-vapour pocket itself.

Conversely, when the mother air-vapour pressure is slightly greater than the air-vapour pocket pressure, the air-vapour bulk can embolize the liquid tight-filled vessel elements with opposite acceleration.

It is interesting to notice, when $\Delta z \approx 10^{-3}\,\mathtt{m}$ and $\boldsymbol{a}.\boldsymbol{k} \approx 10^{6}\,\mathtt{m\,s^{-2}}$, we obtain a transfer time $t \approx 4.4 \times 10^{-5}\mathtt{s}$ corresponding to the ultrasonic frequency $\omega = t^{-1} \approx 20\,\mathtt{kHz}$. The fast accelerations of air-vapour gas through micropores can thus generate ultrasounds and may explain the acoustical measurements obtained in experiments (Milburn and Johnson (1966); Tyree and Dixon (1983)).

The viscosity and diffusion prevailing inside pit membranes and into micro-channels substantially decrease the acceleration value previously estimated in the case of perfect motions. The magnitude of the viscosity of simple wetting fluids increases when they are confined between solid walls, and there is a direct correlation between the air-seeding threshold and the pit pore membranes' diameters (Jansen et al. (2009)). However, the acceleration magnitude is so large for perfect motions that it remains very important for viscous fluids and semi-permeable bordered-pit membranes.

2.3. *Some remarks on motions in tight-filled vessels and in liquid-water thin-films*

It is interesting to compare the behaviour of liquid motions both in tight-filled vessels and liquid-water thin-films.

When the vessel elements are tight-filled with crude sap, the liquid-water motions are Poiseuille flows (Zimmermann (1983)). The Poiseuille flow is *rigid* and the pressure effects are propagated onto the vessel walls.

When the vessel elements are embolized, liquid-water thin-films damp the xylem walls. Equation (1.6) governs the liquid motion along the thin-film, and as we have seen in Subsection 1.4, allows to obtain a non-negligible flow rate. The flow rate can increase or decrease depending on the local disjoining pressure value. The tree's versatility allows it to adapt to the disjoining pressure gradient effects by opening or closing the stomata and the curvature of pit pores, so that the bulk pressure in micropores can be more or less negative and so, the transport of water in tight-filled vessels is differently dispatched through the stem parts.

It is noteworthy that embolized vessels fundamentally contribute to the crude-sap ascent and to the refilling of the tree. Thus, as indicated by Zimmermann (1983), it is not surprising that the heartwood may contain liquid under positive pressure while in the sapwood the transpiration stream moves along a gradient of negative pressure. Embolized vessels creating liquid-water thin-films with non-negligible flows may provide an important contribution to tree refilling by watering the heartwood. The heartwood liquid-water may also fill the vessel elements at negative pressure through the bordered-pit membranes connecting the thin-films and the mother liquid-bulk at negative pressure.

It is noticeable that if we replace the flat surfaces of the vessels (at molecular scale) with corrugated surface, it is much easier to obtain the complete wetting requirement, which is otherwise only partial, as indicated at the beginning of the section; thus, trees can avoid having very high energy surfaces. However, they are still internally wet if crude sap flows through wedge-shaped corrugated pores. The wedge does not have to be perfect on the nanometric scale to significantly enhance the amount of liquid flowing at modest pressures, the walls being considered as plane surfaces endowed with an average surface energy.

To be efficient for sap transportation, the tubes' diameters should be as wide as possible;

because of the micron size of the xylem tubes, this is not the case. Consequently, the tracheary elements' network must be important. As the sap movement is induced by the transpiration across micropores located in tree leaves and the transpiration is bounded by micropores' sizes, it seems natural to surmise that the diameters of vessels must not be too large to generate a sufficient sap movement.
Recent advances in tree hydraulics have demonstrated that, contrary to what was previously believed, embolism and repair may be far from routine in trees. Trees can recover partially or totally from the deleterious effects of water stress until they reach a lethal threshold of cavitation (Delzon and Cochard (2014)). This result can be related with the fact that thin films with a thickness greater than the pancake-layer's one are highly stable; this behaviour is different from bubble stability, which is associated with a saddle point (Gouin and Slemrod (1995)).

3. Topmost trees

The main reason of the maximum size that trees can reach is not well understood (Koch et al. (2004)). Amazingly, the above studies for thin films allow to estimate a boundary value for thin-films' altitude. The boundary value corresponds to the limit of validity of the disjoining pressure concept. Other mechanical or biological constraints may suggest adaptation to height-induced costs, but our model nevertheless limits the maximum height of trees. The tallest trees are not the ones with the largest demand for tension; it is rather dry climate shrubs that demand it. This observation seems to be in accordance with the possible existence of thin-films in embolized vessels at high elevation. For tall trees, we have seen that liquid thin-films and disjoining pressure may indirectly contribute to the xylem refilling. The thickness of the liquid thin-film decreases when its altitude increases. The xylem refilling is not possible anymore when the liquid thin-film breaks down. The liquid thin-film disrupts when thickness reaches the pancake layer thickness-value. The pancake layer of liquid thin-films was presented in Subsection 1.2; our aim is to point out a numerical simulation connected with physical data of xylem such that previous results provide a value of maximum height for a vertical water thin-film wetting xylem wall.
We consider water at 20°Celsius. The main physical coefficients are $\rho_l = 998$ kg m^{-3}, $c_l = 1.478 \times 10^3$ m s^{-1}, $\gamma = 72.5 \times 10^{-3}$ N m^{-1} (Handbook of Chemistry and Physics (1984)). As indicated in Section 2, the Young contact angle between the xylem wall and the liquid-vapour water interface is $\theta \approx 50°$. Other necessary physical coefficients due to molecular interactions are proposed in Gouin (2009, 2012) and used for the numerical calculations and we can compare calculations obtained for trees with the sketch of the pancake layer thickness presented in Fig. 3:
In the upper graph of Fig. 6 we present the free energy graph $G(h)$ associated with trees' xylem walls. Due to $h > (1/2)\,\sigma_l$ - where $\sigma_l = 2.8 \times 10^{-10}$ m stands for the water molecular diameter (Israelachvili (1992)) - point W is obtained by an interpolation associated with the concave part of the G-curve. Point P follows from the drawing of the tangent line issued from W to the G-curve. In the lower graph of Fig. 6, we present the disjoining pressure graph $\Pi(h)$. The real physical part of the disjoining pressure graph corresponds to $\partial\Pi/\partial h < 0$. The hypothetic part, where $\partial\Pi/\partial h > 0$, is also obtained by Derjaguin et al. (1987). The reference length is of the same order as σ_l. The total pancake thickness h_p is about one nanometer order corresponding to a good thickness value for a high-energy surface (de Gennes (1985)); consequently in the tall trees, at high level, the thickness of the liquid thin-film must be of a few nanometers. Point P on the lower graph corresponds to point P on upper graph. The lower graph is theoretically obtained

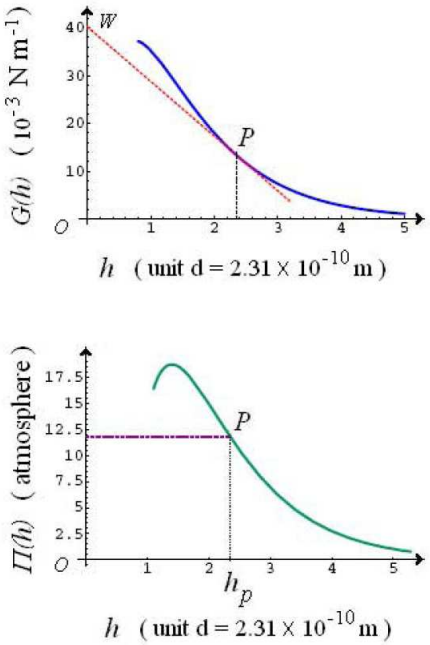

FIGURE 6. *The maximum height of trees. Upper graph*: $G(h)$-graph. The unit of x-axis graduated by h is $d = 2.31 \times 10^{-10}$ m ; the unit of $y-$axis is 10^{-3} N m^{-1}. *Lower graph*: $\Pi(h)$-graph. The unit of x-axis graduated by h is $d = 2.31 \times 10^{-10}$ m; the unit of $y-$axis is one atmosphere (From Gouin (2011), page 21).

in Gouin (2011), and is in accordance with experimental curves obtained in the literature. Let us note that the crude sap is not pure water; its vapour-liquid surface tension has a lower value than the surface tension of pure water and it is possible to obtain the same spreading coefficients with less energetic surfaces.
When x_P corresponds to the altitude of the pancake layer, $\Pi(h_p) \simeq \rho_l\, g\, x_P$. At this altitude, we must approximatively add 20 meters corresponding to the ascent of sap due to capillarity and osmotic pressure, and reading on the lower graph of Fig. 6, we obtain a maximum film height of approximatively 140 meters (20 + 120 meters) corresponding to 12 atmospheres, which is of the same level order as the topmost trees, as a giant, 128 meter-tall eucalyptus or a 135 meter-tall sequoia (Flindt (2006)).

4. Conclusion

Theoretical developments in the field relating to the disjoining pressure could explain sap rise relatively to the cohesion-tension theory and also explain how sap might rise notwithstanding the existence of discontinuities or embolisms in the tracheary elements. The disjoining pressure of liquid thin-films being the exhaust valve allowing for crude sap ascent, the embolized vessels constitute a necessary network for the watering and recovery of tall trees (Lampinen and Noponen (2003) argued that embolisms were necessary for the ascent of sap). The molecular forces can create liquid-water thin-films on the walls of xylem when the micropore pressures are versatilely adapted thanks to pit membranes. Nevertheless, simple in vivo observations of the nanometre thickness of the liquid-water thin-films are not easy to implement and the direct measurement difficulties prevent their detection. The progression of MEMS technology (Tabeling, ed. (2004)), and

tomography (Herman (2009)), may provide a new route towards this goal.
As done in Stroock et al. (2014), we ask questions: "if plants can do it, why don't we? Why do human technologies not use liquids under tension?" We can conclude that if these biophysical considerations are experimentally verified, they would seem to prove that trees can be an example to use technologies for liquids under tension connected with liquids in contact with solid substrates at nanoscale range. They would provide a context in which nanofluid mechanics points to a rich array of biological physics and future technical challenges.

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The aim of the paper is to analyze the results obtained in the theoretical physical chemistry literature that are useful to explain the watering of tall trees in the ascent of crude sap and the refilling of xylem microtubes. All the calculations already obtained are not performed again but only directly presented together with the bibliography explaining the detailed calculations (Derjaguin et al. (1987); Gouin (1998); Gouin and Gavrilyuk (2008); Gouin (2008, 2009, 2011, 2012)), both for the sake of simplicity and to make the demonstrations more accessible. In this paper, we have to note that the apparent incompatibility between the model in Gouin (1998) and the cohesion-tension theory is solved. The model allows to explain aspects of sap movement which the classical cohesion-tension theory was hitherto unable to satisfactorily account for, e.g. the refilling of the vessels in spring, in the morning, or after embolism events as well as the compatibility with thermodynamics' principles.

A general view of the watering of trees.

Trees are engines running on water, and on carbon dioxide when exposed to sunlight. These circumstances pose multiple challenges for crude sap transfer (Holbrook and Zwieniecki (2005); Stroock et al. (2014)): unlike animals, plants miss an active pump to move liquids along their vascular system. The crude sap - mainly liquid water absorbed and transported through trees - ascents thanks to the negative pressure generated by the evaporation of water from the leaves. Additively, trees operate a second vascular system - phloem sieve tubes - for the circulation of metabolites though their living tissues, with positive pressures, and elaborated sap flows passing from leaves to roots. Measurements of the pressure within the terminal xylem vessels illustrate an extraordinary consequence of trees' behaviour for moving liquid water up to their leaves: the pressure must be negative and the liquid water is under tension although it seems prone to cavitation.
Trees do not approach the ultimate tensile strength of liquid water during transpiration (Herbert and Caupin (2005)). Nonetheless, the liquid water columns do break in xylem microtubes. Multiple types of measurements provide evidence for the cavitation of the liquid water in the xylem: cavitation events in the xylem microtubes seem to have been acoustically detected with ultrasonic transducers pressed against the external surface of the trees (Milburn and Johnson (1966); Tyree et al. (2003)). The porous vessel walls can prevent the gas bubbles from spreading and allow the flow to take alternate paths around the emptied segments (Mercury and Shmulovich (2013)). The principal flow of water during transpiration goes to evaporation through stomata on the underside of the leaves. The pores - or bordered pits - connecting adjacent segments in the xylem vessels pass through the vessel walls, and are bifurcated by bordered-pit membranes which are thin physical fluid-transmitters. Pit membranes in pores are of fundamental importance at nanometric scales; applying the Laplace formula, the pressure difference across them can easily be of the order of 1 to 10 MPa (Meyra et al. (1966)). They play a crucial role in maintaining the integrity of the water transport system (Jansen et al. (2009)). When wetted on both sides, the bordered-pit membranes allow the liquid-water flow to pass through. These membranes seem to allow for unusual transport processes in trees: flows of liquid water at negative pressures in the xylem counter flows of elaborated sap at positive pressure in the phloem. In the leaves, these membranes serve as capillary seals that allow for a difference in pressure to exist between the liquid in the xylem and the gas phase outside. In the stem, the bordered-pit membranes also serve as seals between

a gas-filled segment and an adjacent liquid-filled segment, and avoid the propagation of massive embolisms when isolating the air-filled xylem tubes from the rest of the xylematic stem (Tyree and Sperry (1989)). Consequently, trees seem to live in unphysical conditions (Zwieniecki and Holbrook (2009)), and to be hydrated, they exploit liquid water in thermodynamically metastable states of negative pressure.

Xylem microtubes constitute the crude-sap watering network. Crude sap contains diluted salts but its physical properties are roughly those of liquid water. In any tree, the crude sap is driven along xylem microtubes; consequently, hydrodynamics, capillarity, and osmotic pressure yield a crude sap ascent of a few tens of meters only (Zimmermann (1983)).

As explained before, the pressure in the water-storing tracheids of leaves can be strongly negative and consequently the pressure in the xylem microtubes of stems can also remain strongly negative (Canny et al. (2007)). This classical explanation of the sap ascent phenomenon in tall trees is known as the well-known cohesion-tension theory propounded in 1893-1895 by Boehm (1893), Dixon and Joly (1894) and Askenasy (1895), followed by a quantitative analysis of the sap motion proposed by van der Honert (1948). According to this theory, the crude sap tightly fills microtubes of dead xylem cells and its transport is due to a gradient of negative pressure producing the traction necessary to lift water against gravity. A main experimental checking on the cohesion-tension theory comes from an apparatus called Scholander pressure chamber (Scholander et al. (1955)): a leaf attached to a stem is placed inside a sealed chamber; compressed air is slowly added to the chamber. As the pressure increases to a convenient level, the sap is forced out of the xylem and is visible at the cut end of the stem. The required pressure is opposite and of equal magnitude to the water pressure in the water-storing tracheids in the leaf. The decrease in the negative pressure is related to the closing of the aperture of microscopic stomata in leaves through which water vapour is lost by transpiration.

Haberlandt (1914) described water-storing tracheids in leaves; they are roundish in shape, and located either at the tips of the veins or detached from transporting xylem. In more recent papers they have been called tracheid idioblats (Foster (1956)). The spacing considered in Pridgeon (1982), is about $2\,\mu\mathrm{m}$ or less at the top of trees as suggested on Fig. 2 of the paper by Koch et al. (2004), which is the right size to prevent cavitation for nucleus germs of the same order of magnitude.

No vessels are continuous from roots to stems, from stems to shoots, and from shoots to petioles. The vessels do not all run neatly parallel and form a network generally up to a few centimeters long. The ends usually taper out; it is very important for the understanding of water conduction to realize that the water does not leave a vessel in axial direction through the very end but laterally along a relatively long stretch where the two vessels, the ending and the continuing ones, run side by side. The vascular bundles of some leaves are surrounded by a bundle sheath, containing a suberized layer comparable to the one of the Casperian strip in the roots (O'Brien and Carr (1970)). This seal separates the apoplast into two compartments, one inside and the other one outside the bundle sheath. The two areas are only connected by the plasmodesmata that connect living cells. The pressure in the intact, water-containing neighbouring tracheids, may still be negative; a considerable pressure drop therefore exists across the pit membranes and the large variations in their structure enhance their important role in xylem transport (Choat et al. (2008)). Pressure chamber measurements cannot be considered as pressure values of the stem xylem without special precautions, simply because they are taken elsewhere. Hydraulically then, the leaf is very sharply separated from the stem. The wet wood area of elms appears to act as a single, giant osmotic cell that is separated from the sapwood area by a semi-permeable membrane. This can be visualized

somewhat like a Traube membrane, as early plant physiologists called it (Traube (1867)).

Problems associated with the cohesion-tension theory and the water recovery in xylem microtubes.

Nonetheless, several objections question and seem to challenge the validity of the cohesion-tension theory, and worse, to preclude the possibility of refilling embolized xylem tubes.

We first refer to the well-known book by Zimmermann (1983). He said: "The heartwood is referred to as a wet wood. It may contain liquid under positive pressure while in the sapwood the transpiration stream moves along a gradient of negative pressures. Why is the water of the central wet core not drawn into the sapwood? Free water, *i.e.* water in tracheids, decreases in successively older layers of wood as the number of embolized tracheids increases. The heartwood is relatively dry *i.e.* most tracheids are embolized. It is rather ironic that a wound in the wet wood area, which bleeds liquid for a long period of time, thus appears to have the transpiration stream as a source of water, in spite of the fact that the pressure of the transpiration stream is negative most of the time. It should be quite clear by now that a drop in xylem pressure below a critical level causes cavitations and normally puts the xylem out of function permanently. The cause of such a pressure drop can be either a failing of water to the xylem by the roots, or excessive demand by transpiration."

Following these comments, at great elevation in trees, the value of the negative pressure increases the risk of cavitation and consequently, the formation of embolisms may cause a definitive break-down of the continuous column of sap inducing leaf death. In Gouin (2008) we take another consideration into account: crude sap is a fluid with a superficial tension γ lower than the superficial tension of pure water, which is about 72.5×10^{-3} N m^{-1} at 20°Celsius as indicated in Meyra et al. (1966); if we consider a microscopic air-vapour bubble with a diameter $2R$ smaller than xylem microtube diameters, the difference between air-vapour pressure P_v and liquid sap pressure P_l is expressed by the Laplace formula $P_v - P_l = 2\,\gamma/R$ (Bruhat (1967)); the air-vapour pressure is positive and consequently unstable bubbles will appear when $R \geq -2\,\gamma/P_l$. For a negative pressure $P_l = -0.6$ MPa in the sap, corresponding to an approximative minimal value of the hydrostatic pressure for embolism reversal in plants of *Laurus nobilis* (Nardini et al. (2011)), we obtain $R \geq 0.24\,\mu$m; then, when all the vessels are tight-filled, germs naturally pre-existing in crude water may spontaneously embolize the tracheids.

Another objection to the confidence in the cohesion-tension theory was also the experiment by Preston (1952) who demonstrated that tall trees survived double saw-cuts, made through the cross-sectional area of the trunk to sever all xylem elements, by overlapping them. This result, confirmed by several authors (e.g. Mackay & Weatherley (1973); Sperry (2013)), does not seem to be in agreement with the possibility of strong negative pressures in the water-tight microtubes. Using a xylem pressure probe, Bailling & Zimmermann (1990) showed that, in many circumstances, this apparatus does not measure any water tension (Tyree et al. (2003)). However, there are other possibilities for the tree's survival (researchers presented some physical evidences for the local refilling that restores embolized conduits by visualizing the conduits with microscope (Canny (1997, 2001); McCully et al. (1998); Holbrook and Zwieniecki (1999)).

A negative argument seems also to come from the crude sap's recovery in embolized xylem tubes. At high elevation in a tree, it does not seem possible to refill a tube full of vapour-gas at a positive pressure when liquid-water must be at a negative pressure. In the xylem, the liquid-water's metastability - due to negative pressures - may persist even

in the absence of transpiration. Consequently, refilling processes pose a tough physical challenge to push the liquid-water back into the xylem vessels: once embolized vessels have reached a nearly full state, is the refilling solution still at positive pressure, in mechanical equilibrium with some remaining air?

Theories of xylem embolism repair.

The refilling process poses a physical challenge and theoretical problems.
The most popular theory has been proposed by Holbrook & Zwieniecki in several papers. Due to the fact that xylem microtubes are generally in contact with numerous living cells (Zimmermann (1983)), they hypothesize that crude sap is released into the vessel lumen from the adjacent living cells in a manner similar to root exudation (Kramer and Boyer (1995)) and they assume that the mechanism for water movement into embolized conduits involves the active secretion of solutes by the living cells. Nonetheless, a survey across species indicated that the root pressure can reach 0.1-0.2 MPa above atmospheric pressure (Fisher et al (1997)) and was the only logical source of embolized vessels' repairing at night in smaller species with well-hydrated soil. The Münch pumping mechanism is invoked but basic challenges for the Münch mechanism still persist (Münch (1930)): osmotic pressures measured in sieve tubes do not scale with the height of a plant as one would expect (Turgeon (2010)) and such scenarios have not yet been empirically verified. Hydraulic isolation is also required to permit the local creation of the positive pressures necessary to force the gas into solution and the embolism removal may be concurrent with tree transpiration (Zwieniecki and Holbrook (1998)). Additively, refilling in the presence of tension in adjacent vessels requires the induction of an energy-dissipating process that locally pumps liquid into the emptied vessels (Canny (1997)) or lowers the water potential in the vessel with the secretion of solutes (Zwieniecki and Holbrook (2009). As a consequence, Canny (1997) and other authors suggested that alternative mechanisms were required.

Alternatively, for slightly compressible liquids, the molecular theory of capillarity, applied to liquid thin-films wetting solid substrates, points out an unexpected behaviour in which liquids do not transmit the pressure to all their connected parts, as it is well known for liquid-bulk parts (Dzyaloshinsky et al. (1961)). Consequently, it is possible to obtain an equilibrium between connected liquid parts where one is at a positive pressure - the pressure in a liquid thin-film - and the other is at a negative pressure - the pressure in the liquid bulk. The vapour-gas phase in contact with the liquid thin-film is at the same positive pressure as the liquid thin-film.
The experiments and model associated with this behaviour correspond to the so-called *disjoining pressure theory* (Derjaguin et al. (1987); de Gennes (1985)). The disjoining pressure theory allows for the equilibrium between liquid-water-bulk parts with negative pressures and vapour-gas-bulk parts with positive pressures. The cohesion-tension theory thus appears to be compatible with the laws of thermodynamics and molecular physics, and the refilling of xylem tubes by the crude sap is not in contradiction with possible phase equilibria at different pressures in the stems.